

The use of serial sections to estimate age-related occlusal variability in arvicolid molars

Laurent VIRIOT

Accepted for publication: 25 Feb., 1995

VIRIOT L. 1996. The use of serial sections to estimate age-related occlusal variability in arvicolid molars. Acta zool. cracov., 39(1): 577-583.

Abstract. Arvicolids wear down their hypsodont molars daily as they feed. This leads to a nearly flat occlusal surface that displays great morphological variability during the animal's life. Earlier work on this topic is reviewed and a mechanical version of the serial section method is proposed to investigate age-related occlusal variability in arvicolid molars. When applied to the occlusal variability of the first lower molars (M_1) of *Pliopotamys minor* from the Hagerman local fauna, the serial section method appears to be an effective way to bring out the major trends in occlusal morphology in the course of molar abrasion. Comparison between the individual abrasion sequence (IASM₁) and the population abrasion sequence (PASM₁) of the M_1 allows us to pinpoint transient details that are not always observable on the molars of a large population.

Key words: Arvicolidae, M_1 , occlusal surface, age variability, serial sections, *Pliopotamys minor*.

Laurent VIRIOT, Paléontologie analytique, Centre des Sciences de la Terre, Université de Bourgogne, 6 Bd Gabriel, 21000 Dijon, France.

I. INTRODUCTION

Voies and lemmings, commonly grouped in the family Arvicolidae (Rodentia, Mammalia), develop highly specialised molars. The occlusal part of the molar becomes nearly flat from the very first days of life because the animal wears down its teeth daily as it feeds. Since they first appeared in the Holarctic fossil record about 5.5 million years ago (REPENNING 1987), more than 140 lineages of arvicolids have been identified on the basis of their evolving dental morphology (CHALINE 1987). These lineages all exhibit four main trends in molar evolution: (1) increase in hypsodonty; (2) increase in the number of triangles (polyisomery sensu THALER 1962); (3) appearance of coronal cementum; (4) loss of roots. In the course of evolution, increased molar hypsodonty involves an increased rate of molar abrasion throughout the animal's lifespan and greater diversity of occlusal morphologies among individuals of the same species.

Unlike shells in animals with accretionary modes of growth (e.g. ammonites, Lamellibranchia, brachiopods), where juvenile morphology can be observed on the adult shell, hypsodont molars exhibit a very special feature: adult wear stages can be obtained by the abrasion of juvenile teeth. This has led to the development of a new method for assessing age-related occlusal variability in arvicolid molars. The serial section method consists in wearing the molars down at regular intervals

to simulate natural abrasion of the crown. Thus, a series of occlusal morphologies obtained by mechanical abrasion of a single molar is termed an individual abrasion sequence of the molar (IASM). Similarly, a series of tooth morphologies obtained by collating occlusal views of the molars of an entire population is known as a population abrasion sequence of the molar (PASM).

A c k n o w l e d g m e n t s. I am grateful to the team of the Museum of Paleontology of Ann Arbor (University of Michigan) and in particular to Philip GINGERICH who allowed me to make sections of a number of juvenile arvicolid molars. Thanks also to Alain FESTEATU for mounting the teeth and to Jean CHALINE, Véronique PARISOT and Christopher SUTCLIFFE for helpful comments and suggestions.

II. REVIEW OF EARLIER WORK ON TOOTH ABRASION SEQUENCES

P o p u l a t i o n a b r a s i o n s e q u e n c e s

In 1975, CHALINE and MICHAUX pioneered a new way of understanding and depicting arvicolid molars. They used a population abrasion sequence, then termed a "demogram", to demonstrate that the wide range of variation in the occlusal morphology of the first lower molar (M_1) of *Mimomys occitanus occitanus* of Sète (France) is related to dimorphism with distinct mimomyan and dolomyan features. In 1977, KOENIGSWALD was the first to depict changes in the M_1 and third upper molar (M^3) occlusal surfaces of *Mimomys* cf. *reidi* of Schambach (Germany), thus showing that morphological changes in the occlusal surface can be accounted for by the reduced height of the crown. In that paper, the author explained that neither tooth length nor width are obviously correlated with morphological changes in the occlusal surface. This descriptive technique was then taken up by RABEDER who, in 1981, produced population abrasion sequences for nine species of *Mimomys*, two species of *Clethrionomys* and three species of *Pliomys*. These works have gained widespread acceptance in that new descriptions of arvicolid populations commonly include a population abrasion sequence (e.g. ESTEBAN AENLLE & LOPEZ MARTINEZ 1987, ESTEBAN & LOPEZ MARTINEZ 1990; KAWAMURA 1988, 1989; BACHELET et al. 1991; KOTLIA & KOENIGSWALD 1992).

I n d i v i d u a l a b r a s i o n s e q u e n c e s

The need to understand "vertical" variability in arvicolid molars had been felt long before. ZEJDA first used artificial abrasion as early as 1960. He demonstrated that "simplex" and "complex" occlusal dimorphism of the M^3 in *Clethrionomys glareolus* is dependent on age and accordingly on the extent of wear of the molar. The technique of making serial sections of arvicolid molars was adopted much later by CHALINE & SEVILLA (1990) for the development of an empirical version of the serial section method.

Comparison of the two methods of artificial abrasion brings out certain problems. ZEJDA embedded the skulls in resin whereas CHALINE and SEVILLA used isolated teeth for abrasion. Arvicolids chew mainly with a longitudinal movement (GRASSÉ & DEKEYSER 1955) and the pendular grating effect caused by these masticatory movements, means that slightly more abrasion occurs at specific points along the rows of teeth: in the centre of the lower row and at the front and rear ends of the upper row. It seems difficult to simulate natural abrasion of several teeth at once because the pendular masticatory movement cannot be reproduced easily. CHALINE and SEVILLA's method therefore seems more suitable, as errors are minimised by using only one tooth at a time. It is regrettable that, in both instances, wear is simulated manually with abrasive paper and the wear interval of 0.5 mm is too great for the study of more primitive arvicolid molars. But the greatest loss of information results from the use of excessively worn molars, because the early mineralised ontogenetic stages of the molar are located at the top of the crown in neonates. This type of study requires the use of molars from the youngest animals possible.

III. MECHANICAL VERSION OF THE SERIAL SECTION METHOD

The mechanical version of the serial section method has been developed with regard to all the drawbacks referred to above. The margin of error has been reduced through a painstaking method for setting the teeth in various resins (for technical details see VIRIOT et al. 1993). The molar is worn down mechanically by a diamond grinding wheel that is lowered using a micrometer screw, and it is then drawn at regular intervals selected by the operator. Initial experiments, carried out for the study of IASM₁ and IASM³ of *Ondatra zibethicus*, produced good results.

IASM analysis provides insight into age-related occlusal variability on the basis of a single molar from a juvenile specimen whose growth is completed by rhizagenesis (hypsoarhizodont growth). However, one molar is sometimes not enough to provide a complete picture of the range of occlusal variation. In the case of *Ondatra zibethicus*, for example, molars are highly hypsodont and two different ones are needed for a full IASM. The serial section method reaches its limits when hypsoarhizodont molars (i.e. with continuous growth) are considered, because the number of crown heights worn down during the animal's lifetime cannot be covered by a single tooth. In such cases an IASM can be obtained, but only by stringing together fractions of the sequence, which means that it is essential to know the age of the individuals whose molars are used.

IV. ABRASION SEQUENCE IN *PLIOPOTAMYS MINOR*

Pliopotamys minor (WILSON, 1933)

During the past 3.75 million years, five chronospecies of muskrat have superseded one another over time, gradually evolving into the present day muskrat (*Ondatra zibethicus*). *P. minor* is the oldest representative of the North American muskrat chronomorphocline: *P. minor* – *P. meadensis* – *O. idahoensis* – *O. annectens* – *O. zibethicus* (NELSON & SEMKEN 1970; SCHULTZ et al. 1972; MARTIN 1979, 1984). *P. minor* is known from the Hagerman and Sand Point local faunas of Idaho (WILSON 1933; HIBBARD 1959; ZAKRZEWSKI 1969, 1974). The origin of the genus *Pliopotamys* is still unclear; ZAKRZEWSKI (1969) and MARTIN (1975) claim that the ancestor of *P. minor* is to be sought in the *Ogmodontomys* stock.

Our study covers thirty M₁s of *P. minor*, selected from hundreds of teeth collected near Hagerman by HIBBARD and preserved in the collections of the University of Michigan Museum of Paleontology (UMMP).

I A S M₁ of *Pliopotamys minor*

The occlusal surface of the M₁ of *P. minor* viewed in section is composed, from back to front, of a nearly rectangular posterior loop, five alternating triangles and a cockscomb anterior loop that becomes rounded with age (Fig. 1).

The M₁ UMMP 53594-01 was worn down and drawn at 0.1 mm intervals at the top of the crown, and then every 0.2 mm to the base of the crown (Fig. 2). The top was investigated at finer intervals than the base of the crown because occlusal morphological drift is usually far more rapid there. The 0 degree of wear displays a simple occlusal morphology, and this is probably the molar of a very young, or even neonate, individual. At this stage, the occlusal surface features a posterior loop, five clearly separate triangles, and a very short bilobed part at the front of the tooth.

Morphological change in the posterior loop during IASM₁

The posterior loop changes from a somewhat oval shape in juveniles to a nearly rectangular shape in older specimens, but overall there is little alteration in shape.

Morphological change in the triangles during IASM₁

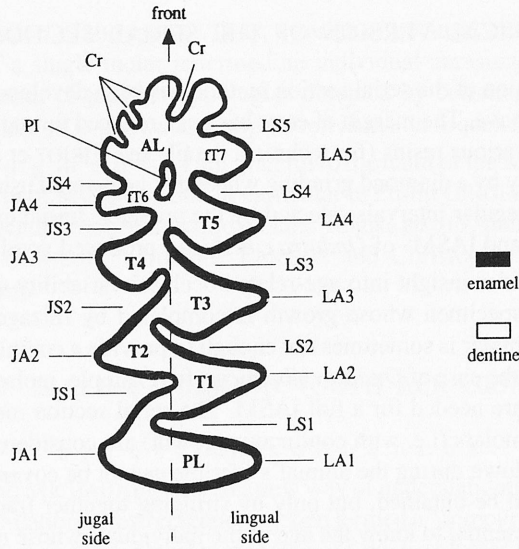


Fig. 1. Occlusal surface of the first lower molar (M₁) of *P. minor*. PL: posterior loop; T: triangle; ft: future triangle; AL: anterior loop; PI: pliopotamyan islet; Cr: crenellations; JA: jugal anticline; JS: jugal syncline; LA: lingual anticline; LS: lingual syncline.

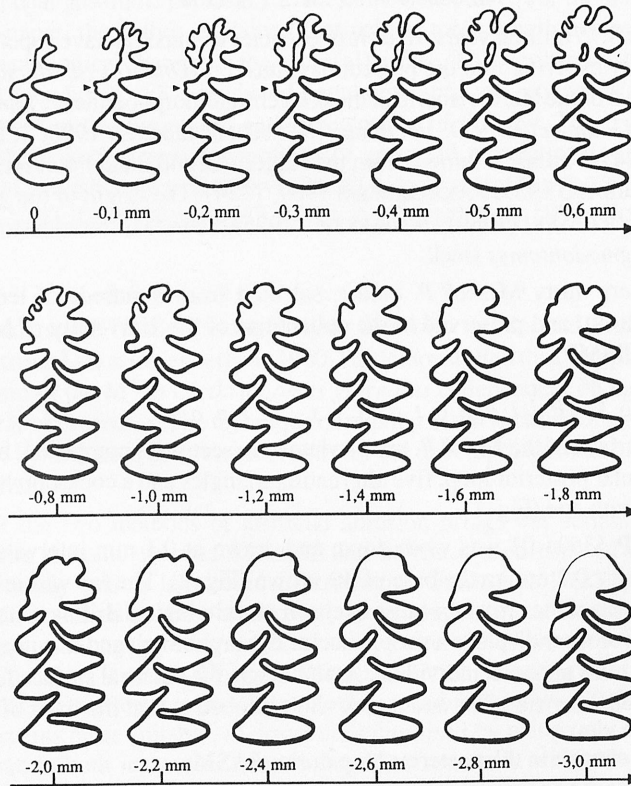


Fig. 2. Individual abrasion sequence of the M₁ UMMP 53594-01. The molar has been drawn every 0.1 mm from the 0 mm to -0.6 mm stages, and then every 0.2 mm from the -0.6 mm to -3 mm stages. The arrows point to the T4 furrow between the 0 mm and -0.4 mm stages. See text for descriptions.

The lingual triangles are larger than the jugal ones, especially in the juvenile stages. During wear, they change from a pointed to a more rounded shape and are always confluent. Triangle 5 is highly asymmetric as the posterior wall bulges far more than the anterior wall. Triangle 4 displays a remarkable feature: from the -0.1 mm to -0.4 mm wear stage, it is split into two protuberances separated by a furrow. This is not a rare structure and is found on the T4 of numerous fossil arvicolid M₁ (e.g. in the genera *Cosomys*, *Mimomys*, *Ogmodontomys*, *Ophiomys*). In 1969, ZAKRZEWSKI (page 23, Text-fig. 8B and 8E) noticed the furrow on T4 and considered it to be like other crenellations of the future T6 (fT6) or of the anterior loop. In fact, the T4 furrow has very special significance in arvicolids; it is an ancestral character that is no longer found in any living descendants. This character could be useful for a discussion of the phyletic relationships of *Pliopotamys*. Lower on the crown, T4 becomes rounded and is clearly different in shape from the other triangles.

Morphological change in the anterior loop of the IASM₁

The anterior loop gains in complexity between the 0 and -0.4 mm stages, and then becomes progressively simpler and is perfectly regular by the -3 mm stage. A crosswise channel, formed by the extension of JS3, virtually splits the anterior loop into two. This channel then closes to form an enamel islet, that can be seen from the -0.3 mm to -0.6 mm stage. The enamel islet has an extended shape and forms an angle of about 5° with the longitudinal axis of the molar. The isolation of enamel within the dentine results from the closure of the deepest part of JS3 by the partial fusion of T4 and fT6. The pliopotamyan islet occurs at the same jugal syncline as the mimomyan islet, but the T4 and the future T6 persist after the islet vanishes, meaning that the two types of islets are intrinsically different. There are numerous crenellations of variable depth on the anterior loop in juveniles. As the tooth is worn down, major crenellations can be made out that testify to far deeper furrows than the others. Two of these major furrows, clearly visible from the -0.6 mm to -2.0 mm stages, can be identified as JS4 and LS5, as they already delimit the future T6 and T7. A further very deep furrow delimits a lobe at the front of T7 that continues almost all the way down to the base of the crown. This furrow is not connected to any known structure. Finally, at the -3 mm wear stage, the anterior loop exhibits a large anterior-jugal enamel free area.

Comparison between the IASM₁ and PASM₁ of *Pliopotamys minor*

A PASM₁ was formed by ranking the thirty molars by decreasing crown height (27 of them are shown in Fig. 3).

P o s t e r i o r l o o p: the posterior loop bulges greatly and is almost angular in some individuals, such as UMMP 53594-02, -13, -15, -14 and -16. This swelling of the posterior loop is found only in juvenile stages.

T r i a n g l e s: T4 is not split in any individuals in this sample, underlining the transient aspect of this character. In addition, the triangles display exactly the same variation as in the previous study.

A n t e r i o r l o o p: the anterior loop displays the most extravagant shapes among juvenile individuals, with variable short crenellations but also deeper ones that in most cases separate the future T6 and T7 (e.g. UMMP 53594-07). In this sample, the presence of the enamel islet, or even of several islets, is far more difficult to interpret. Specimen UMMP 53594-02 seems to form an enamel islet by closure of LS4, which is most unusual. Two or three islets are commonly found, but as a result of subdivision of the main channel into smaller secondary islets. Lengthwise, the enamel islet forms an angle on the jugal side of between 0° and 10° with the longitudinal axis of the molar.

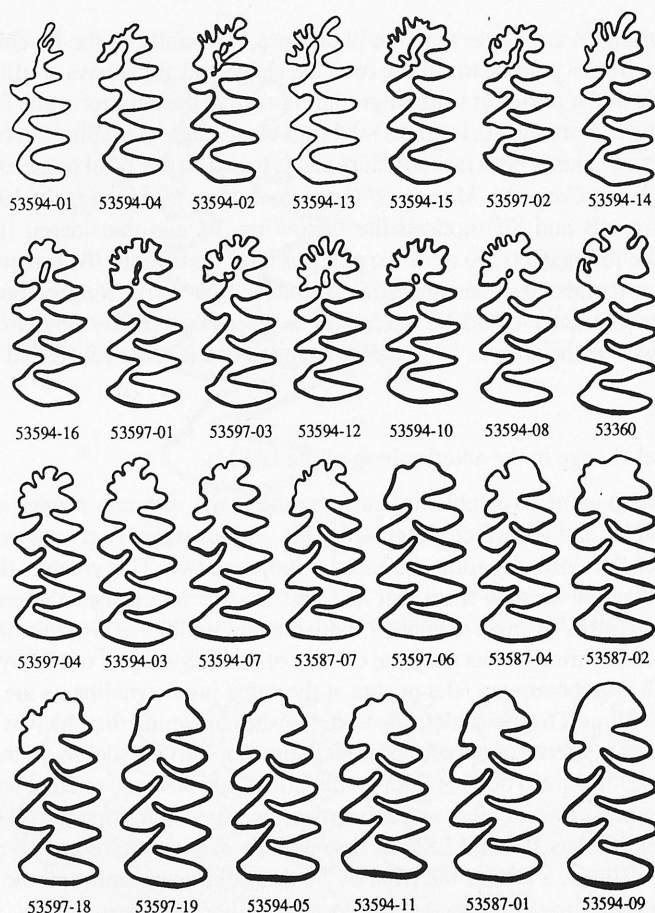


Fig. 3. Population abrasion sequence of the M₁ of *P. minor* from the Hagerman local fauna. Twenty-seven M₁s are ranked by decreasing order of crown height. See text for descriptions.

V. CONCLUSIONS

Variability in occlusal morphology in a sample of molars from the same species can largely be accounted for by the differential extent of tooth wear. However, some factors of intraspecific variability seen from the PASM₁ are not related to the degree of molar abrasion: (1) the difference in size of molars at the same wear stage is particularly clear when comparing UMMP 53360 and UMMP 53597-04; (2) polymorphism of the anterior loop in the early stages of wear, which can be seen especially between UMMP 53594-02 and UMMP 53594-13. The age independent variability component can be estimated through comparison of IASM and PASM from several populations of the same period. The serial section method is an effective way to bring out the major trends in occlusal morphology and to pinpoint transient details in the course of molar abrasion in arvicolids.

REFERENCES

- BACHELET B., ESTEBAN AENLLE J., LOPEZ MARTINEZ N. 1991. Révision des populations de *Mimomys* de petite taille (Rodentia, Mammalia) du Pliocène Supérieur d'Europe Sud-Occidentale. *Geobios*, **22**: 349-360.

- CHALINE J. 1987. Arvicolid data (Arvicolidae, Rodentia) and evolutionary concepts. *Evolutionary Biology*, **21**: 237-310.
- CHALINE J., MICHAUX J. 1975. Microévolution chez les campagnols (Arvicolidae, Rodentia): la cladogenèse *Mimomys stehlini* – *Dolomys hungaricus*. [In:] Problèmes actuels de paléontologie (Évolution des vertébrés). CNRS Ed., Paris. Colloque **218**: 749-759.
- CHALINE J., SEVILLA P. 1990. Phyletic gradualism and developmental heterochronies in a European Plio/Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). [In:] O. FEJFAR, W.-D. HEINRICH (eds.) – Evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia). Geological Survey, Prague, pp: 85-98.
- ESTEBAN AENLLE J., LOPEZ MARTINEZ N. 1987. Les Arvicolidés (Rodentia, Mammalia) du Villanyen récent de Casablanca 1 (Castellon, Espagne). *Géobios*, **20**: 591-623.
- ESTEBAN F. J., LOPEZ MARTINEZ N. 1990. Villanyian arvicolids from Moreda and Casablanca I, Spain, with special reference to their position in a Plio-Pleistocene faunal succession. [In:] O. FEJFAR, W.-D. HEINRICH (eds.) – Evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia). Geological Survey, Prague, pp: 99-114.
- GRASSÉ P.-P., DEKEYSER P. L. 1955. Ordre des Rongeurs. [In:] *Traité de Zoologie*, **17**: 1321-1525. Masson & Cie, Paris.
- HIBBARD C. W. 1959. Late Cenozoic microtine rodents from Wyoming and Idaho. *Papers of the Michigan Academy of Science, Arts, and Letters*, **44**: 3-40.
- KAWAMURA Y. 1988. Quaternary rodent faunas in the Japanese Islands (Part 1). *Memoirs of the Faculty of Science, Kyoto*, **53**: 1-348.
- KAWAMURA Y. 1989. Quaternary rodent faunas in the Japanese Islands (Part 2). *Memoirs of the Faculty of Science, Kyoto*, **54**: 1-235.
- KOENIGSWALD W. v. 1977. *Mimomys cf. reidi* aus der villafranchischen Spaltenfüllung Schambach bei Treuchtlingen. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, München*, **17**: 197-212.
- KOTLIA B. S., KOENIGSWALD W. v. 1992. Plio-pleistocene Arvicolids (Rodentia, Mammalia) from Kashmir intermontane basin, Northwestern India. *Paleontographica*, **223**: 103-135.
- MARTIN L. D. 1975. Microtine rodents from the Ogallala Pliocene of Nebraska and the early evolution of the Microtinae in North America. [In:] G. R. SMITH, N. E. FRIEDLAND (eds.) – Studies on Cenozoic paleontology and stratigraphy, C. W. HIBBARD Memorial Volume, The University of Michigan, Ann Arbor., **3**: 101-111.
- MARTIN L. D. 1979. The biostratigraphy of arvicoline rodents in North America. *Transactions of the Nebraska Academy of Sciences*, **7**: 91-100.
- MARTIN L. D. 1984. Phyletic trends and evolutionary rates. [In:] M. DAWSON, H. GENOWAYS (eds.) – J. E. GUILDAY memorial volume. Carnegie Museum of Natural History, Special publications, **8**: 526-538.
- NELSON R. S., SEMKEN H. A. 1970. Paleoeological and stratigraphic significance of the muskrat in Pleistocene deposits. *Geological Society of America Bulletin*, **81**: 3733-3738.
- RABEDER G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Österreich, Wien*, **8**: 1-373.
- RENNING C. A. 1987. Biochronology of the microtine rodents of the United States. [In:] M. O. WOODBURN (ed.) – *Cenozoic Mammals of North America: geology and biostratigraphy*. University of California Press, Berkeley, pp: 236-268.
- SCHULTZ C. B., TANNER L. G., MARTIN L. D. 1972. Phyletic trends in certain lineages of Quaternary mammals. *Bulletin of the University of Nebraska State Museum*, **9**: 183-195.
- THALER L. 1962. Campagnols primitifs de l'ancien et du nouveau monde. [In:] Problèmes actuels de paléontologie (Évolution des vertébrés). CNRS Ed., Paris. Colloque **104**: 387-398.
- VIRIOT L., CHALINE J., SCHAAF A., LE BOULENGÉ E. 1993. Ontogenetic change of *Ondatra zibethicus* (Arvicolidae, Rodentia) cheek teeth analyzed by digital image processing. [In:] R. A. MARTIN, A. D. BARNOSKY (eds.) – *Morphological change in Quaternary Mammals of North America*. Cambridge University Press, pp: 373-391.
- WILSON R. W. 1933. A rodent fauna from later Cenozoic beds of southwestern Idaho. *Contributions to Paleontology, Carnegie Institution of Washington Publication* **440**: 117-135.
- ZAKRZEWSKI R. J. 1969. The rodents from the Hagerman local fauna, Upper Pliocene of Idaho. *Contributions from the Museum of Paleontology, University of Michigan* **23**: 1-36.
- ZAKRZEWSKI R. J. 1974. Fossil Ondatrini from western North America. *Journal of Mammalogy* **55**: 284-292.
- ZEIDA J. 1960. The influence of age on the formation of the third upper molar in the bank vole *Clethrionomys glareolus* (SCHREBER, 1780) (Mammalia, Rodentia). *Folia Zoologica*, **9**: 159-166.

